Acta Geologica Polonica, Vol. 66 (2016), No. 3, pp. 299–312
DOI: 10.1515/agp-2016-0015

The heterodonty in euselachian sharks from the Pennsylvanian of Nebraska

MICHAŁ GINTER

Faculty of Geology, University of Warsaw, Żwirki i Wigury 93, 02-089 Warszawa, Poland.
E-mail: m.ginter@uw.edu.pl

ABSTRACT:

Ginter, M. 2016. The heterodonty in euselachian sharks from the Pennsylvanian of Nebraska. *Acta Geologica Polonica*, **66** (3), 299–312. Warszawa.

Among the rich material of chondrichthyan microremains from the Indian Cave Sandstone (Upper Pennsylvanian, Gzhelian) near Peru, Nebraska, USA, housed at the Carnegie Museum of Natural History, there occur almost sixty teeth representing Euselachii. They belong to at least seven species, presenting various types of heterodonty. Two new species are described, viz. *Ossianodus nebraskensis* gen. et sp. nov., whose dentition is similar to that of certain Mesozoic hybodonts, and *Sphenacanthus tenuis* sp. nov. with minute teeth of protacrodont design. Most of the euselachian teeth served to crush or grind prey, and some had the potential to clutch, but cutting teeth are absent from the fauna.

Key words: Euselachii; Dentition; Carboniferous; Indian Cave Sandstone; USA Midcontinent.

INTRODUCTION

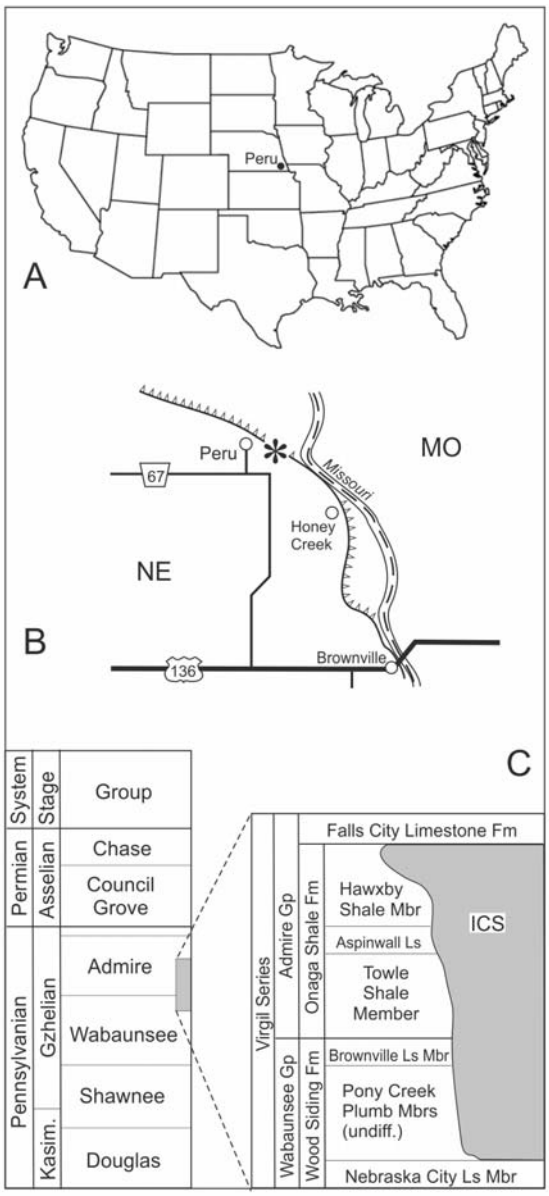
In 1974, Clair R. Ossian presented his Ph.D. dissertation in which he described numerous fossils, mainly of vertebrate and botanical origin, from the locality at Peru, Nemaha County, Nebraska (Ossian 1974). The fossils were found in the Indian Cave Sandstone, supposed to represent the Upper Pennsylvanian (Text-fig. 1). Among the very diverse vertebrate macro- and microfossils – counted in thousands – he reported about 20 chondrichthyan tooth-based taxa, together with chondrichthyan dermal denticles, spines, and putative calcified cartilage fragments. Although the fossils were found in sandstone bodies, Ossian recovered them by chemical processing, using acetic acid. Many chondrichthyan teeth in the collection are beautifully preserved, displaying only slight, superficial abrasion. Larger vertebrate skeletal fragments, however, are usually broken.

Among the Chondrichthyes, Ossian (1974) identified a few cladodontomorphs, at least two xenacanthiforms, euselachians (with a previously undescribed hybodont which he named "*Hybodus nebraskensis*"), various euchondrocephalans (orodonts?, petalodonts, eugeneodontiforms, and holocephalans), and iniopterygians. Unfortunately, the dissertation has never been published and the proposed new species have never been formally described.

During my visit in 2003 to the Carnegie Museum of Natural History in Pittsburgh I came across a collection of chondrichthyan teeth, apparently from the same locality and horizon (SE of Peru, Nebraska, Indian Cave Sandstone) as that studied by Ossian. The labels state that it was collected by David S. Berman (currently Curator Emeritus of that museum) in 1971, i.e., during the time of preparation of Ossian's dissertation. The teeth are perfectly prepared and, as in the case of Ossian's ma-

terial, most of them are only slightly abraded. The taxonomic content is similar to that listed above, but petalodonts and iniopterygians are missing. The quality and diversity of these teeth is so high that some of them were illustrated in the Handbook of Paleoichthyology, vol. 3D (Ginter et al. 2010, figs. 3, 6) as examples of various tooth forms in Palaeozoic chondrichthyans.

Among the material from the Carnegie Museum are numerous teeth which are comparable with Ossian's "*Hybodus nebraskensis*" with greater or lesser degrees of certainty. A few of them are almost identical to that illustrated by Ossian (1974, pl. 4, figs 7, 8), with a typical high, hybodont crown, but there are also other, generally similar teeth, but with lower (protacrodont-like) and often more asymmetrical crowns. I propose that the former and the latter teeth represent the same hybodont species, characterised by a highly heterodont dentition (monognathic heterodonty), and describe it here under a new name of *Ossianodus nebraskensis* gen. et sp. nov.



Text-fig. 1. A – Position of Peru, Nebraska, against the outline of USA. B – The study area (asterisk) on the edge of Missouri River valley near Peru. NE, Nebraska, MO, Missouri; 67, 136, road numbers. C – Stratigraphic position of the Indian Cave Sandstone body (ICS) near Peru. B, C, after Fischbein *et al.* (2009)

In his dissertation, Ossian (1974, figs 1, 2, 5, 6) illustrated two types of teeth with protacrodont crowns, as *Protacrodus* cf. *P. vetustus*, but they look somewhat different to those included here in *O. nebraskensis* and probably belong to the representatives of the genus *Sphenacanthus*, viz. *S. carbonarius* (Giebel, 1848) and *S. tenuis* sp. nov. The rest of euselachian teeth from the Pennsylvanian of Peru belong to a *Lissodus*-like shark and a few other, yet unidentified, forms. All of them present some heterodonty, but its degree varies from species to species. This problem will be discussed at the end of this paper.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; CM, Carnegie Museum of Natural History, Pittsburgh, USA; NMS, National Museums of Scotland, Edinburgh, Scotland, UK.

GEOLOGICAL SETTING

The Indian Cave Sandstone (ICS) at Peru is one of several large sandstone bodies (10–30 m thick and 1–10 km wide) in Upper Pennsylvanian marine-dominated cyclothems of Midcontinent USA (Nebraska, Kansas, Oklahoma, Missouri, Iowa) which indicate major shifts in facies tracts and significant fluctuations in relative sea level (Fischbein *et al*. 2009). Ossian (1974) interpreted the ICS as an ancient constructional delta, thereby reflecting prevailing opinions on the origins of sandstone bodies in the Midcontinent and Appalachian Basin in the period of preparation of his dissertation. After 1990, however, many such sandstone bodies were reinterpreted as incised valley fills on the basis of sediment body geometries and lithofacies analysis, and these reinterpretations revealed a richer record of depositional system responses to sea-level change than was previously envisaged (e.g., Archer *et al*. 1994). Fischbein *et al*. (2009) demonstrated that the ICS is a fluvial to estuarine incised valley fill constrained below by a sequence boundary and above by a maximum flooding surface.

ICS lithosomes in southeastern Nebraska, between Peru and Indian Cave State Park, are linear bodies, as

much as 2000 m wide and 30 m thick, incised into pre-existing cyclothems (such as Onaga Shale Formation, see Fischbein *et al*. 2009, figs 2A, 4), and have relatively steep sides and flat bases. They include crudely fining-upwards successions of trough cross-bedded sandstones, interpreted as tidally-influenced fluvial deposits, overlain by upper estuarine heterolithic facies, with local coals, and a restricted trace fossil assemblage. The age of formation of ICS bodies is interpreted as Gzhelian.

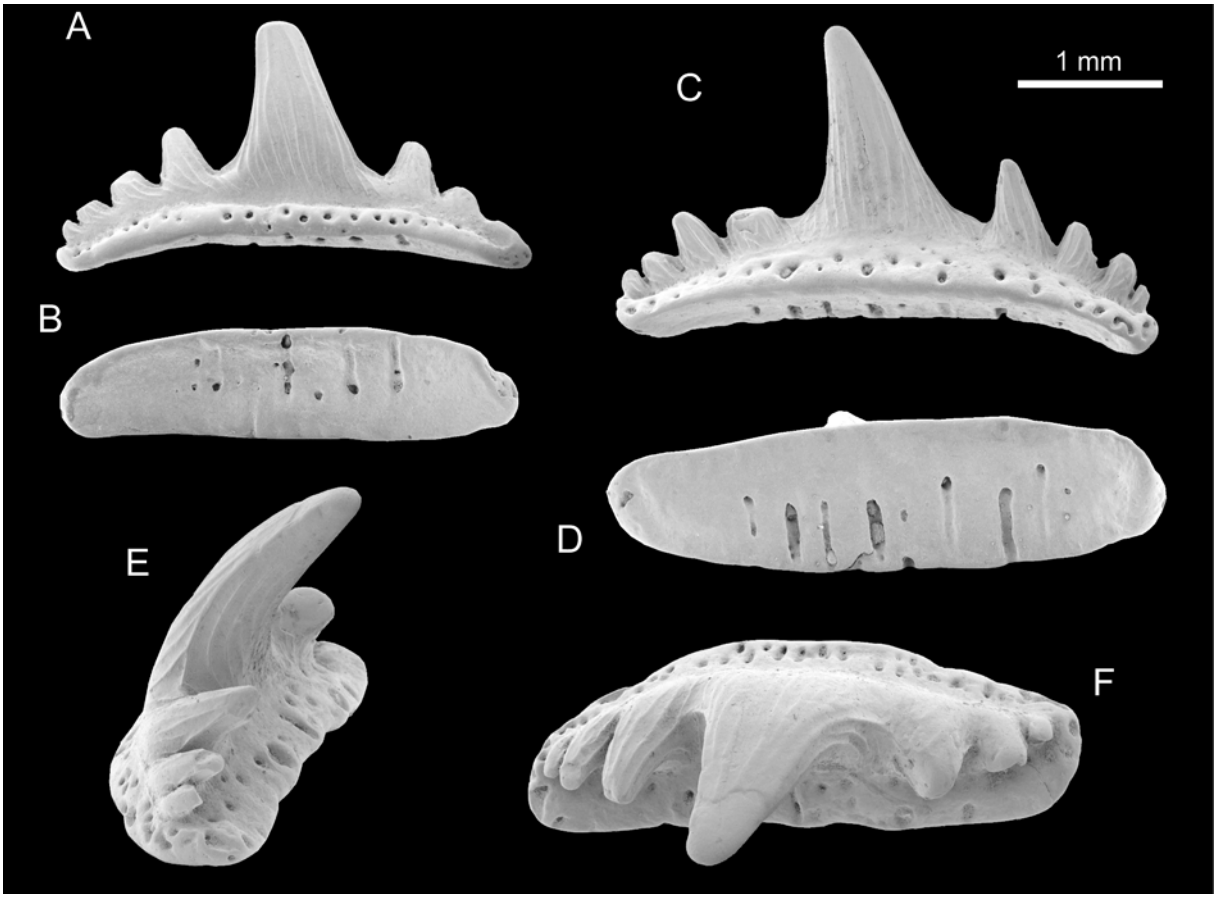
It is unknown to me exactly from which of several ICS sites south-east of Peru the hybodont material, housed at the Carnegie Museum and described below, comes. Almost 2000 teeth referred by Ossian (1974) to "*Hybodus nebraskensis*" were collected at his sites 2 and 3, "channel lag deposits", located between ca 250 and 400 m south of the "base mark", situated on "a very large block of sandstone which has fallen from the cliff at a point approximately 3400 feet [ca 1 km] west-northwest of the intersection of the flood control levee and the railroad embankment south of Peru, Nebraska" (Ossian 1974, p. 315). On the same page, Ossian described these sites as "main vertebrate collection site" and "the only other vertebrate collection site at Peru", respectively. This being the case, it is reasonable to assume that the specimens from the Carnegie Museum collection were recovered from rocks found in one of these two Ossian's sites.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Order Hybodontiformes Maisey, 1975
Superfamily Hybodontoidea Owen, 1846
Family Hybodontidae Owen, 1846
Genus *Ossianodus* gen. nov.

TYPE SPECIES: *Ossianodus nebraskensis* gen. et sp. nov.

ETYMOLOGY: In honour of Dr Clair Russell Ossian who was the first to discover the specimens of this genus.



Text-fig. 2. Teeth of *Ossianodus nebraskensis* gen. et sp. nov. from the Upper Pennsylvanian of Peru, Nebraska. A, B – CM 44547a, in labial and aboral views. C, D – holotype, CM 44547b, in lingual and aboral views. E, F – CM 44547e, in lateral and oral views. Scale bar = 1 mm

DIAGNOSIS: Hybodont shark with a heterodont dentition; tooth-base forming a shallow, gently arched plate, extending beyond the crown base on all sides; both orolingual and orolabial regions of the base perforated with a horizontal row of pores; crown moderately to strongly asymmetrical, composed of six to nine cusps, which may be thin and high, to lower and broad, to very low and pyramidal; all the cusps cristated almost up to their tips on the labial and lingual faces.

REMARKS: The teeth of *Ossianodus* gen. nov., and especially those with high crowns, resemble the dentition of the classic Mesozoic members of the genus *Hybodus* Agassiz, 1837, based on articulated specimens, such as *H. reticulatus* Agassiz, 1837 (see Agassiz 1837-43, vol. 3, pl. 22a, figs 22, 23, pl. 24, fig. 26; Maisey 1987, figs 1, 10, 16, 18), *H. basanus* Egerton, 1845 (Maisey 1983, figs 7, 18), and *H. fraasi* Brown, 1900. It is not surprising then that Ossian (1974) attributed the hybodont teeth found at Peru to *Hybodus* and named the new species "*Hybodus nebraskensis*". Since that time, Maisey (1987) erected a new genus, *Egertonodus*, based on non-dental characters, and placed former *Hybodus basanus* and *H. fraasi* (the latter tentatively) in it. The crown of *Ossianodus* gen. nov. seems to be more similar to that of *Hybodus* sensu stricto, because *Egertonodus* possesses a sigmoidal curvature of the median cusp (see, e.g., Rees 2008), a character absent from both *Hybodus* and *Ossianodus*. However, if the identification of all the teeth, as suggested here, is correct, the heterodonty of the new hybodont from Peru is greater than in both *Hybodus* and *Egertonodus* (see the description below), and therefore, it deserves a new generic name.

Ossianodus nebraskensis sp. nov.
(Text-figs 2, 3)

1974. *Hybodus nebraskensis* n. sp.; Ossian, pp. 122, 123, pl. 4, figs 7, 8.
2010. "undescribed heterodont hybodontiform"; Ginter *et al*., fig. 6A–D.

ETYMOLOGY: From the type locality near the town of Peru, Nebraska.

HOLOTYPE: Tooth, CM 44547b, from the Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska, USA.

MATERIAL: 29 teeth (1st morphotype: 22, 2nd morphotype: 5, 3rd morphotype: 2); Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska, USA.

DIAGNOSIS: As for genus.

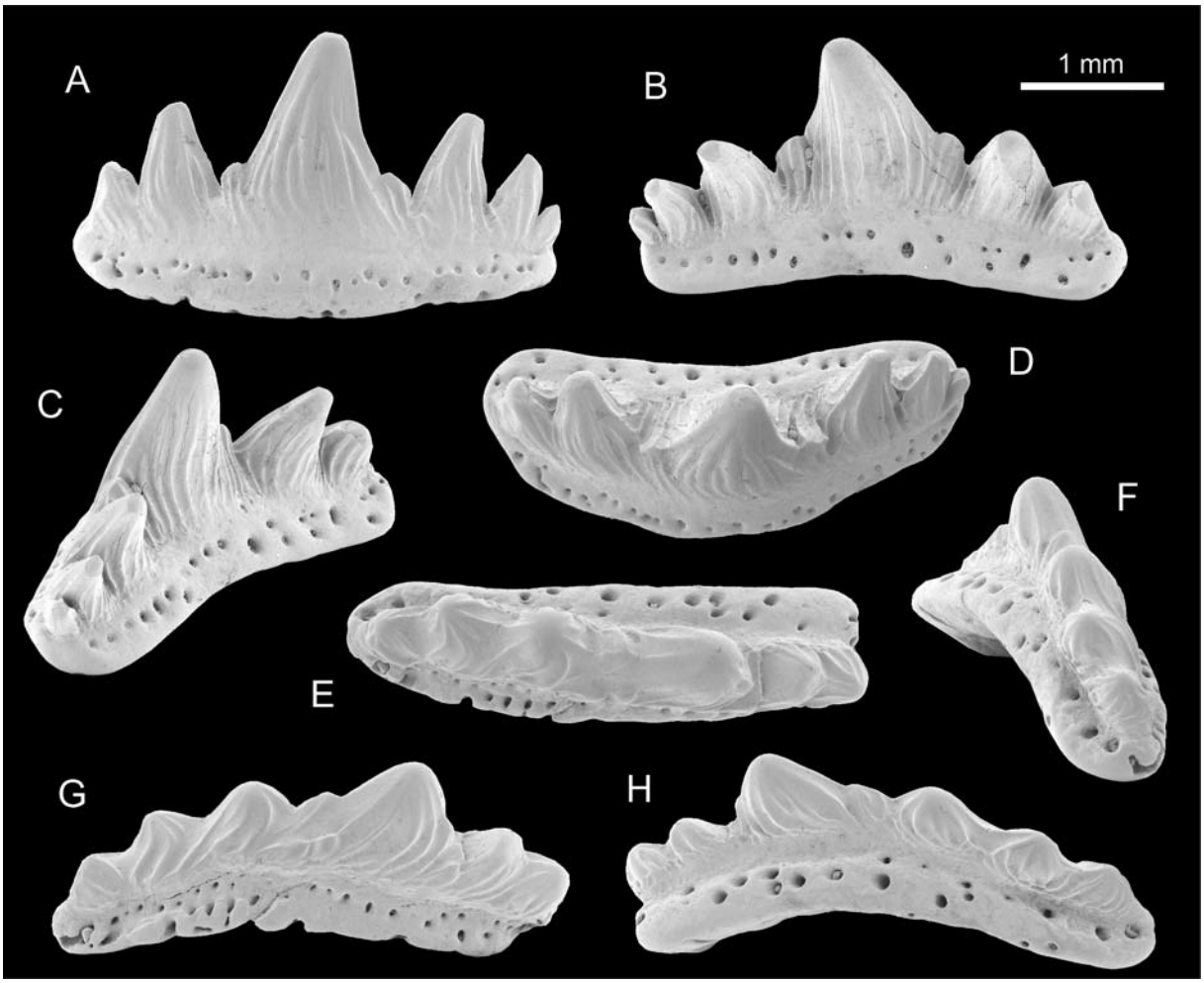
DESCRIPTION: In the material from Nebraska, there are at least six different tooth forms with hybodont-like and protacrodont-like crowns. However, only three of them are considered here to potentially belong to *Ossianodus nebraskensis* gen. et sp. nov., and they will be described first.

All of these three forms have almost the same shape and structure of the base. It is a relatively thin, mesio-distally elongated plate, with rounded ends, from the center of which projects the crown. The base is bent into a gentle curve in occlusal view along the labio-lingual axis. The aboral surface is smooth, only in its labial portion a few labio-lingual grooves for nutritive vessels are present. Because only parts of the grooves are visible, it is quite possible that before shedding and probable abrasion of a tooth they were completely covered by a thin layer of dentine and opened only at the labial rim. In any case, it is obvious that they are situated much shallower in this region, than in the lingual area which is devoid of any trace of foramina or grooves. The oral side is perforated by numerous canal openings, many of which are placed irregularly, but a single, horizontal row of uniform, small pores extending on the labial and lingual sides, very near to the crown, can be distinguished. Articulation devices are absent.

The first, most common type of tooth crown (Text-figs 2, 8A) is characterised by a relatively slender, labio-lingually compressed median cusp (breadth at the base to height ratio about 1:2) and three to four lateral cusps of similar shape on each side. Typically of hybodont teeth, the size of lateral cusps gradually diminishes mesially and distally away from the median cusp. The median cusp may be slightly inclined distally.

The second type of crown (Text-fig. 3A–D) differs from the first by broader cusps (breadth to height about 2:3), and fewer lateral cusps (no more than three on each side). Often, the median cusp is provided with ear-like lateral projections (auricles), as if a new generation of lateral cusps was about to appear. Such teeth are less elongated mesio-distally and slightly reniform in oral view.

The third type of crown (Text-figs 3E–H, 8B) is protacrodont-like, with low, pyramidal cusps (breadth to height 1:1). This type may be very asymmetrical, with a strong distal inclination of the median cusp and a larger number of lateral cusps on the mesial side. Also, if a lateral „ear" is present, it occurs on the mesial side of the median cusp.



Text-fig. 3. Teeth of *Ossianodus nebraskensis* gen. et sp. nov. from the Upper Pennsylvanian of Peru, Nebraska. A-D, CM 44547c, in labial, lingual, oblique lateral and oral views. E-H, CM 44547d, in oral, lateral, labial and lingual views. Scale bar = 1 mm

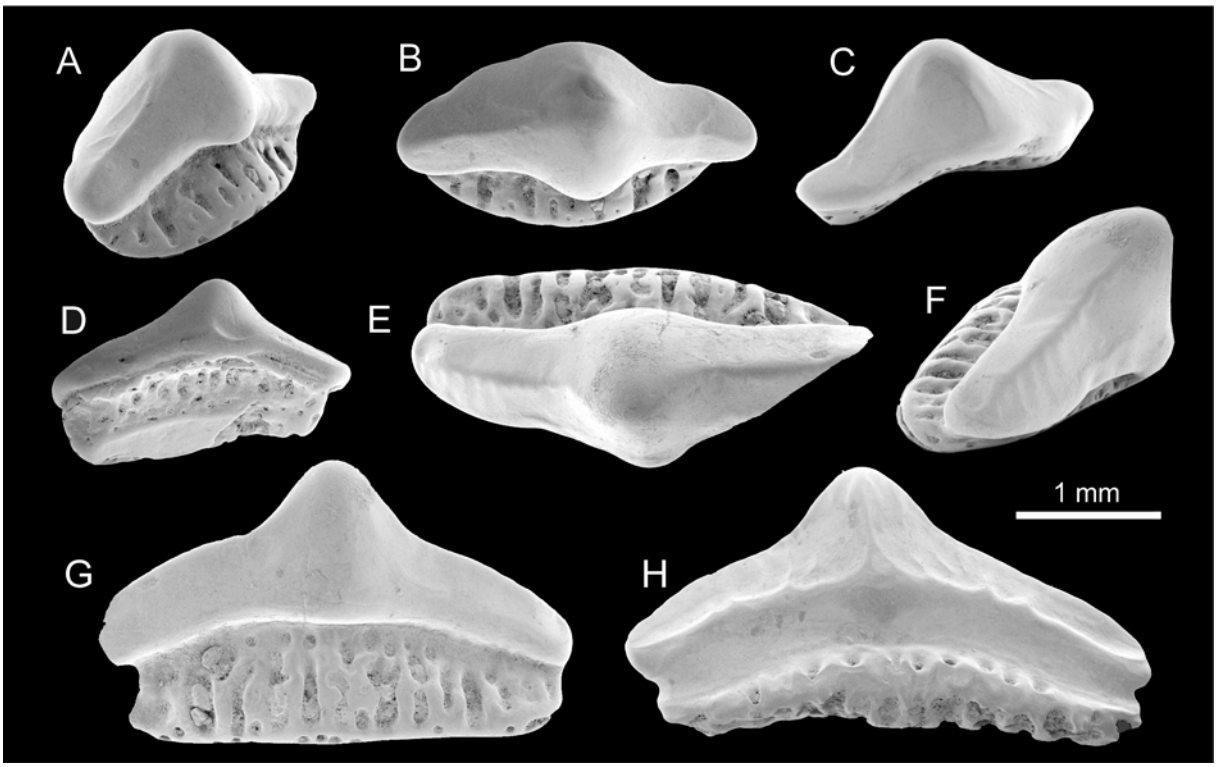
In all the above types of crowns the cusps are moderately to coarsely cristated. The cristae almost join at the cusp apices and some of them bifurcate basally. It seems that in the first type the ornamentation is less pronounced. The average width of the teeth is about 3 mm.

REMARKS: *Ossianodus nebraskensis* gen. et sp. nov. is the oldest shark whose dentition is composed, at least in part, of teeth with typical, high hybodont crowns. Such teeth are otherwise unknown from the pre-Triassic rocks (Duffin in Ginter *et al*. 2010, p. 89). The teeth most similar to these are those of *Egertonodus basanus* from the Early Cretaceous. However, the bases in *E. basanus* are apparently flat, and not arched (Maisey 1983, fig. 18; Cappetta 2012, fig. 36), and the teeth of *Egertonodus* are a few times larger than those of *Ossianodus* (compare Text-figs 8A and F). As mentioned above, the postulated heterodonty of *O. nebraskensis* is greater than in *E. basanus*. In the latter, only the smaller, postero-lateral teeth have somewhat lower crowns and the asymmetry gently increases from the symphysis towards the angular part of a jaw. In *O. nebraskensis* there are probably three clearly different shapes of crown and only the common form of the bases suggests that they belong to the same species.

OCCURRENCE: Carboniferous, Upper Pennsylvanian, Gzhelian, USA (SE Nebraska).

Family Lonchidiidae Herman, 1977
Genus *Lissodus* Brough, 1935

The presence of *Lissodus* in the Palaeozoic has been questioned in the past (e.g. Rees and Underwood 2002; Koot *et al*. 2013) and other generic names were proposed, but still those propositions should be considered



Text-fig. 4. Teeth of *Lissodus* sp. from the Upper Pennsylvanian of Peru, Nebraska. A-C – CM 44545c, in oblique lingual, oral and oblique labial views. D – CM 44545d, in labial view. E-G – CM 44545e, in oral, lateral and lingual views. H – CM 44545f, in labial view. Scale bar = 1 mm

as unfinished. Rees (2008) removed *Lissodus* from the Lonchidiidae, but did not give any new proposition for its assignment at the family level. Therefore, I follow here the classification used by Duffin (e.g., in Ginter *et al*. 2010). However, the state of preservation of the material only allows me to identify the specimens from Peru as *Lissodus sensu lato*, in its older sense.

Lissodus sp. 1
(Text-fig. 4)

MATERIAL: Eleven abraded teeth.

DESCRIPTION AND REMARKS: Typically for this genus, the tooth-crowns of *Lissodus* sp. 1 are composed of a prominent, but low median cusp and rather short lateral wings, sloping mesially and distally. No lateral cusplets are present. The median cusp overhangs the base on both lingual and labial sides (Text-fig. 4A–C). The labial peg is present, but rather moderately developed (Text-fig. 4F). The teeth are evidently abraded, so the ornamentation of the crown, consisting of the main occlusal, mesiodistal crest and several low ridges transversal to it, is observed in only a few specimens. Usually the crown surface looks as almost completely smooth.

The base is of the classic euselachian type (sensu Ginter *et al*. 2010), with the canal openings and grooves present in the orolingual and basolabial areas (Text-fig. 4A, D, G). The heterodonty is minor, restricted to the width of the teeth (compare Text-figs 4B and 4E).

The combination of features of *Lissodus* sp. 1 from Peru: symmetrical teeth, clearly differentiated median cusp, no lateral cusplets or crenulation, small labial peg with no accessory cusplets, distinguishes it from all Palaeozoic *Lissodus*-like forms. It is relatively similar to the symmetrical (putatively anterior) teeth of *Omanoselache hendersoni* from the Permian of Oman (Koot *et al*. 2013, fig. 6A–D) which are characterised by smooth crowns without lateral cusplets. However, the median cusp in *O. hendersoni* is very weakly differentiated from the lateral wings, if at all. Moreover, if the identification of Koot *et al*. (2013) is correct, the lateral teeth of *O. hendersoni* are asymmetrical, whereas none of the specimens of *Lissodus* sp. 1 from Peru shows any significant degree of asymmetry.

Ossian (1974) did not notice and figure teeth of *Lissodus* sp. 1. Only one tooth, illustrated as "*Orodus hemiplicatus"* (Ossian 1974, pl. 5, figs 3, 4), is comparable to the material described here, but its median cusp is lower and less differentiated than in *Lissodus* sp. 1.

Lissodus sp. 2
(Text-fig. 7J–K)

MATERIAL: One well preserved tooth crown.

DESCRIPTION AND REMARKS: This isolated tooth crown resembles to some extent those of *Lissodus zideki* (Johnson, 1981) from the Lower Permian of Texas. Its occlusal crest is slightly crenulated, the median cusp is weakly differentiated from the rest of the crown, on its labial and ligual faces there occurs a transversal ridge. The labial peg is evident, albeit partly broken, with tubercles reminiscent rather of *L. lopezae* Soler-Gijón, 1997, than of *L. zideki*. The other probable difference is the presence of several delicate secondary ridges, transversal to the occlusal crest, on the lateral wings of *Lissodus* sp. 2. Such ridges are apparently missing from the teeth of *L. zideki*.

Euselachii incertae ordinis
Family Sphenacanthidae Maisey, 1982
Genus *Sphenacanthus* Agassiz, 1937

Sphenacanthus tenuis sp. nov.
(Text-fig. 5)

ETYMOLOGY: Latin *tenuis* = small, slender.

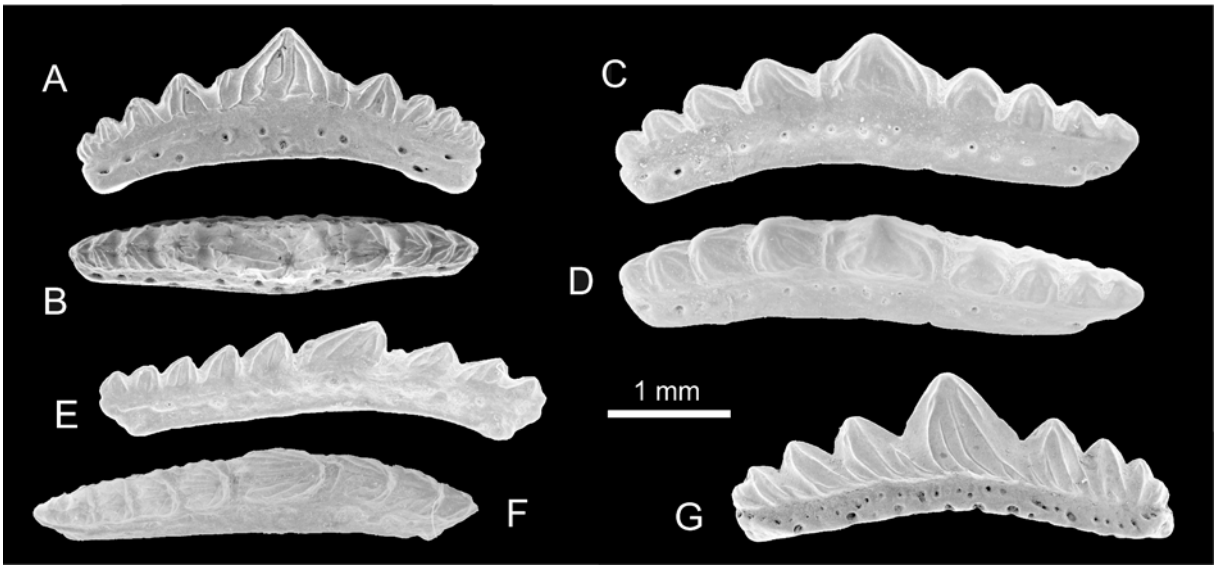
HOLOTYPE: Tooth, CM 44547f, from the Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska, USA.

MATERIAL: Six perfectly preserved teeth; Upper Pennsylvanian, Gzhelian, Indian Cave Sandstone, SE of Peru, Nebraska, USA.

DIAGNOSIS: Small and slender teeth with protacrodont crowns, symmetrical or with the cusps slightly inclined distally. Four lateral cusplets on each side of the prominent, pyramidal median cusp in symmetrical specimens; five cusplets on mesial side and three on distal side in the most asymmetrical specimens. Base relatively deep, arched, with lingual extension very narrow or missing.

DESCRIPTION: All of the teeth of *Sphenacanthus tenuis* sp. nov. from Peru are complete and perfectly preserved. They are relatively small (width 2.5–3.0 mm, height 1 mm), of general protacrodont design, with the median, pyramidal cusp clearly differentiated. Some of them are symmetrical (Text-fig. 5A, B), and others display various degrees of asymmetry (Text-fig. 5C–G; compare Ossian 1974, pl. 4, figs 5, 6).

REMARKS: The teeth of *S. tenuis* are smaller than most of the teeth of *Ossianodus nebraskensis* gen. et sp. nov. and lack the parapet surrounding the crown. They are similar in form to those of *Sphenacanthus serrulatus* Agassiz, 1837 (see Text-fig. 8D, E), but are much smaller, as the width of the teeth of *S. serrulatus* from Scotland usually exceeds 10 mm. Dick (1998) suggests that in one of the Scottish specimens there also occur narrower teeth with only one pair of lateral cusplets. However, such teeth were found neither in Ossian's



Text-fig. 5. Teeth of *Sphenacanthus tenuis* sp. nov. from the Upper Pennsylvanian of Peru, Nebraska. A, B – holotype, CM 44547f, in lingual and oral views. C, D – CM 44547g, in lingual and oral views. E, F – CM 44547h, in lingual and oral views. G – CM 44547i, in labial view; this tooth may actually belong to *Ossianodus nebraskensis* gen. et sp. nov. Scale bar = 1 mm

(1974) collection from Peru nor in that presented here. There could be three reasons of such a difference: (1) the dentitions of *S. serrulatus* and *S. tenuis* are actually different despite the similarity of individual teeth; (2) the alleged narrow teeth of *S. serrulatus* are in fact only middle parts of originally wider teeth; (3) narrower teeth of *S. tenuis* do exist but are so rare that they were overlooked by Ossian and are coincidentally absent from the much poorer Pittsburgh collection.

From the teeth of *S. carbonarius* (Giebel, 1848), those of *S. tenuis* sp. nov. differ by their smaller size, the reduced lingual extension of the base, and the larger number of lateral cusplets.

OCCURRENCE: Carboniferous, Upper Pennsylvanian, Gzhelian, USA (SE Nebraska).

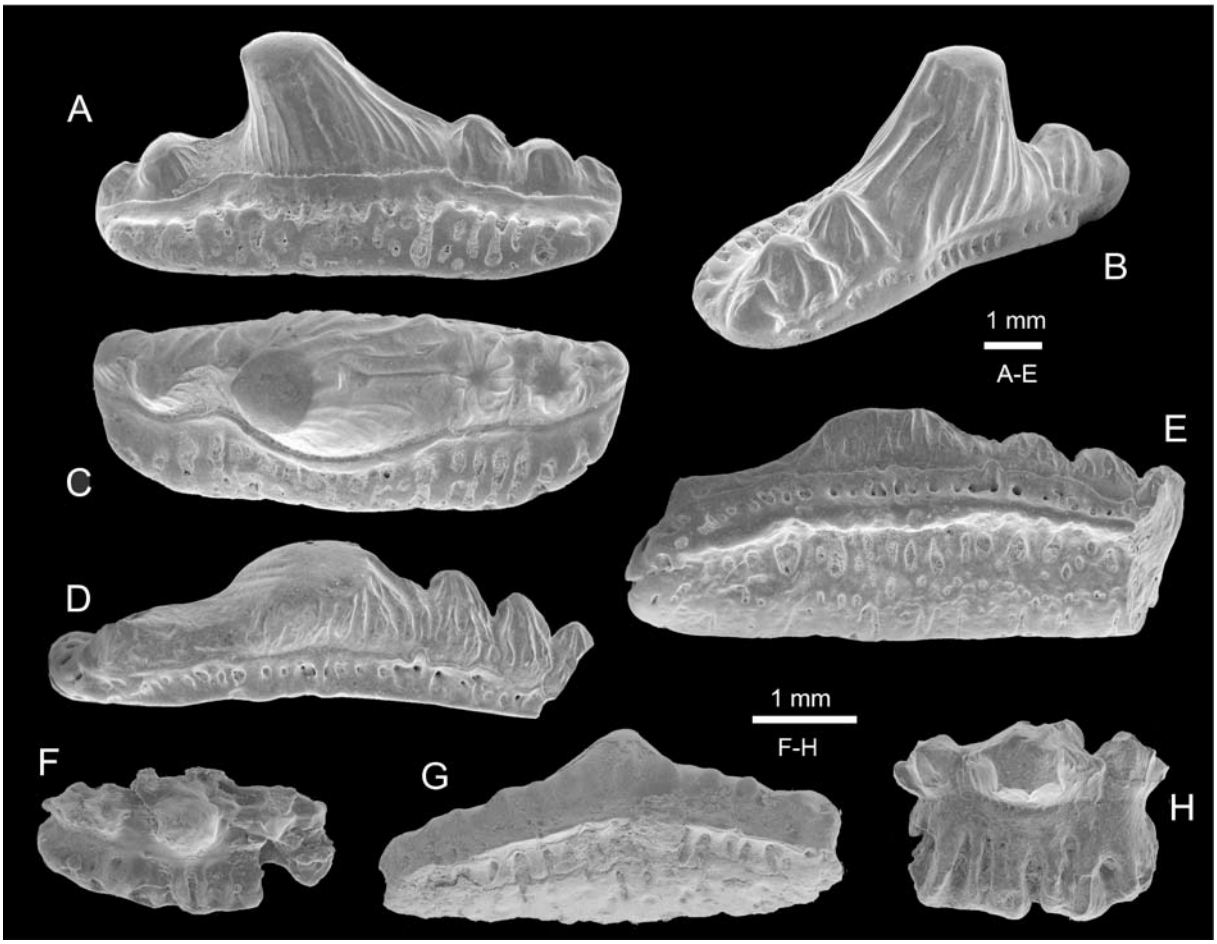
Sphenacanthus carbonarius (Giebel, 1848)
(Text-fig. 6)

MATERIAL: Three teeth.

DESCRIPTION: In the material, there occur two specimens with almost complete bases but partly abraded crowns and one fragmentary tooth. The teeth are of protacrodont design, with thick robust cusps and a relatively high median cusp. They are the largest euselachian teeth in the collection; the base width almost reaches 10 mm.

The best preserved tooth (Text-fig. 6A–C) has a broad median cusp whose basal part occupies about one third of the base. Its height, before abrasion, could have been about 4 mm. The cusp is slightly inclined distally. On the crown flanks, there are three mesial and two distal pyramidal lateral cusplets, each of which is much smaller than the median cusp. The cusplets progressively decrease in height mesially and distally. All the cusps are ornamented with coarse cristae, joining at the cusp apex.

The base is of the euselachian type, with a single, horizontal row of foramina on its labial side (Text-fig.



Text-fig. 6. Teeth of *Sphenacanthus carbonarius* (Giebel, 1848) from the Upper Pennsylvanian of USA. A-E, from Peru, Nebraska. A-C, CM 44547j, in lingual, oblique labial and oral views. D, E, CM 44547k, in labial and aboral views. F-H, from Pittsburgh, Pennsylvania (= *Hybodus allegheniensis sensu* Lund 1970). F, CM 19135b, in oral view. G, CM 19135c, in basal view. H, CM 19135d, in oral view. Scale bar = 1 mm

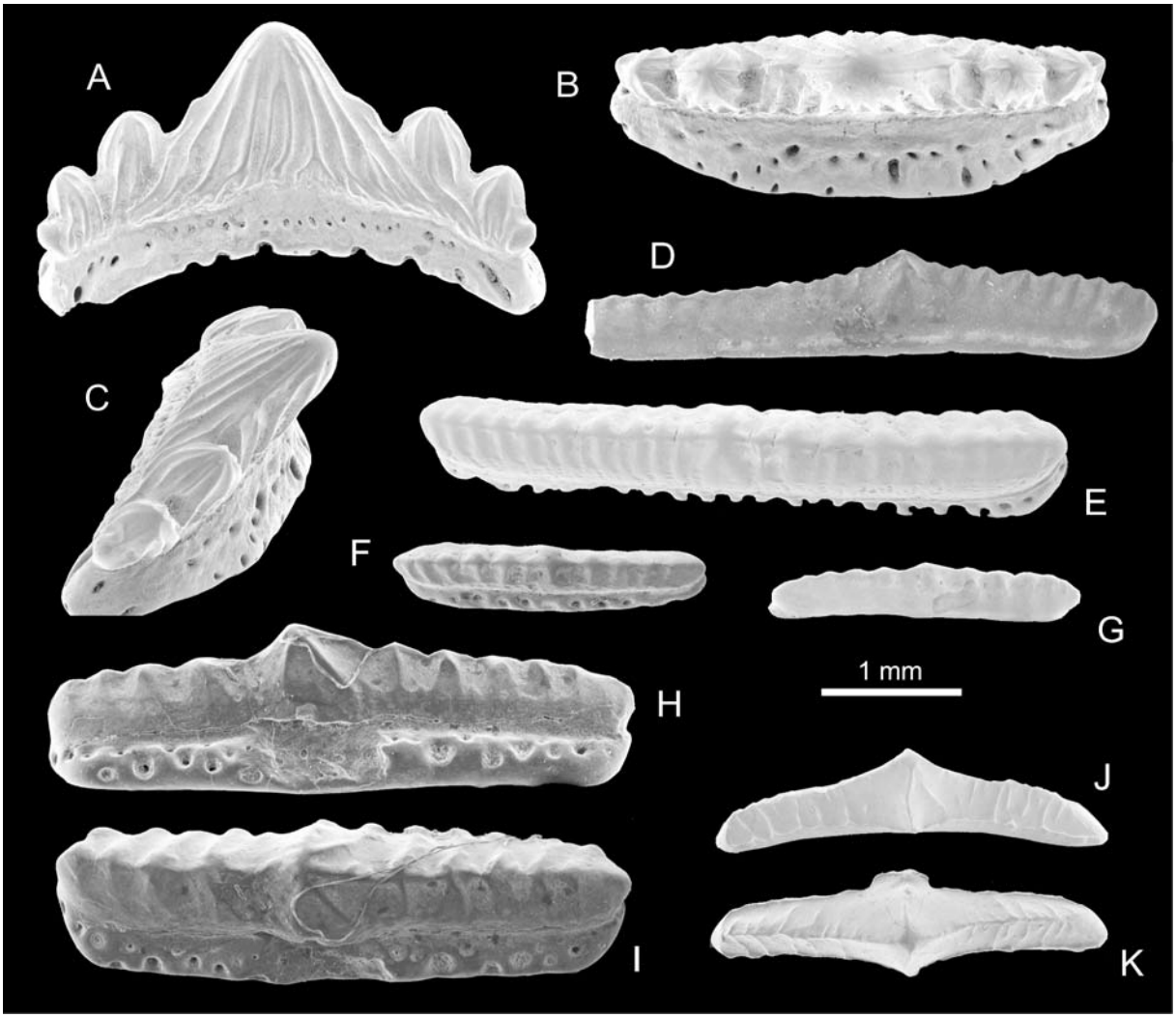
6D) and a deep basolabial depression (Text-fig. 6E). The lingual extension of the base is well developed and distinctly separated from the crown (Text-fig. 6A, B).

REMARKS: The teeth are similar to the material of *S. carbonarius* from the Upper Pennsylvanian of the Puertollano Basin, Spain (Soler-Gijón 1997, pl. 1, fig. 5; see also illustrations in Ginter *et al*. 2010, fig. 94), but they are about twice as large as the average Spanish specimen. This difference, however, may be treated as minor. Soler-Gijón (1997, p. 143) included *Hybodus alleghe-niensis* Lund, 1970, from Pennsylvania, in the synonymy list of *S. carbonarius*. The width of the single tooth illustrated by Lund (1970; see Text-fig. 8C) is about 9 mm and its form is comparable to that of *S. carbonarius* from Peru, Nebraska. The other teeth from Pennsylvania, bearing the same label and collection number (CM 19135), not illustrated by Lund (1970) but figured herein (Text-fig. 6F–H) are smaller and closer in shape and diversity to the material from Spain.

OCCURRENCE: All occurrences of *S. carbonarius* as understood by Soler-Gijón (1997) and updated by Ginter et al. (2010) represent Late Pennsylvanian, Gzhelian and, perhaps, Kasimovian. Teeth of this type were found in Czech Republic, Germany (Wettin near Halle, type locality; Saar-Nahe Basin), central Spain (Puertollano Basin), and USA (SW Pennsylvania; SE Nebraska).

Euselachii gen. et sp. indet. 1
(Text-fig. 7A–C)

MATERIAL: Three teeth.



Text-fig. 7. Teeth of various euselachians from the Upper Pennsylvanian of Peru, Nebraska. A-C, Euselachii gen. et sp. indet. 1, CM 44547l, in labial, oral and lateral views. D-I, Euselachii gen. et sp. indet. 2. D, CM 44547m, in labial? view. E, CM 44547n, in oral view. F, G, CM 44547o, in oral and labial views. H, I, CM 44547p, in lingual and oral views. J, K, *Lissodus* sp. 2, CM 44545g, isolated crown in lingual? and oral views. Scale bar = 1 mm

DESCRIPTION AND REMARKS: These teeth resemble to some extent the forms attributed here to *O. nebraskensis* gen. et sp. nov., but they are absolutely symmetrical with an extremely broad median cusp and two much smaller, rather more dome-like than pyramidal cusps on each side. All the cusps are coarsely cristated. The auricles on the median cusp, or initial stages of new cusplets, especially characteristic of the second type of *O. nebraskensis* crown, occur on the sides of the median cusp and on the outer sides of the lateralmost cusps. The base in these teeth is rather deep, strongly arched, with a short lingual extension, which clearly distinguishes them from *O. nebraskensis*.

Euselachii gen. et sp. indet. 2
(Text-fig. 7D–I)

MATERIAL: Five teeth.

DESCRIPTION AND REMARKS: The teeth of this species are in a form of a bar with numerous low, pyramidal cusps, ornamented with a few coarse cristae, almost entirely fused to each other except for their tips. The median cusp is broader and slightly higher than the other cusps which are generally equal in size. The crown gently lowers laterally away from the median cusp. All the encountered teeth are at least slightly asymmetrical. In most cases the number of lateral cusps on one side (mesial?) is higher than on the other: 11+:9 (Text-fig. 7D, part of the longer side is broken); 10:9 (Text-fig. 7E); 6:4 (Text-fig. 7H, I, the largest tooth). Even in the smallest tooth (Text-fig. 7F, G) in which the number of cusps on each side is equal, one of the sides is slightly thicker and higher. The base is of the euselachian type, flat, with a very short lingual extension. The width of the base is subequal to the crown.

The only Carboniferous teeth known to me the general shape of which is comparable to the teeth described here are: *Orodus angustus sensu* Davis (1883, see also Ginter et al. 2010, fig. 102C) and *Mesodmodus exsculptus* St. John and Worthen (1875), at least the specimen reillustrated by Duffin in Ginter *et al*. (2010, fig. 91A). However, the width of *O. angustus* is almost 40 mm, whereas the teeth from Peru do not exceed 5 mm. Moreover, they lack the tubular dentine layer on the crown, definitely present in *O. angustus*. Also the specimen of *M. exsculptus* is larger (23 mm wide?) and its base appears to be convex, with the median part slightly higher than the lateral ends, which makes it different from the flat base in the teeth from Nebraska.

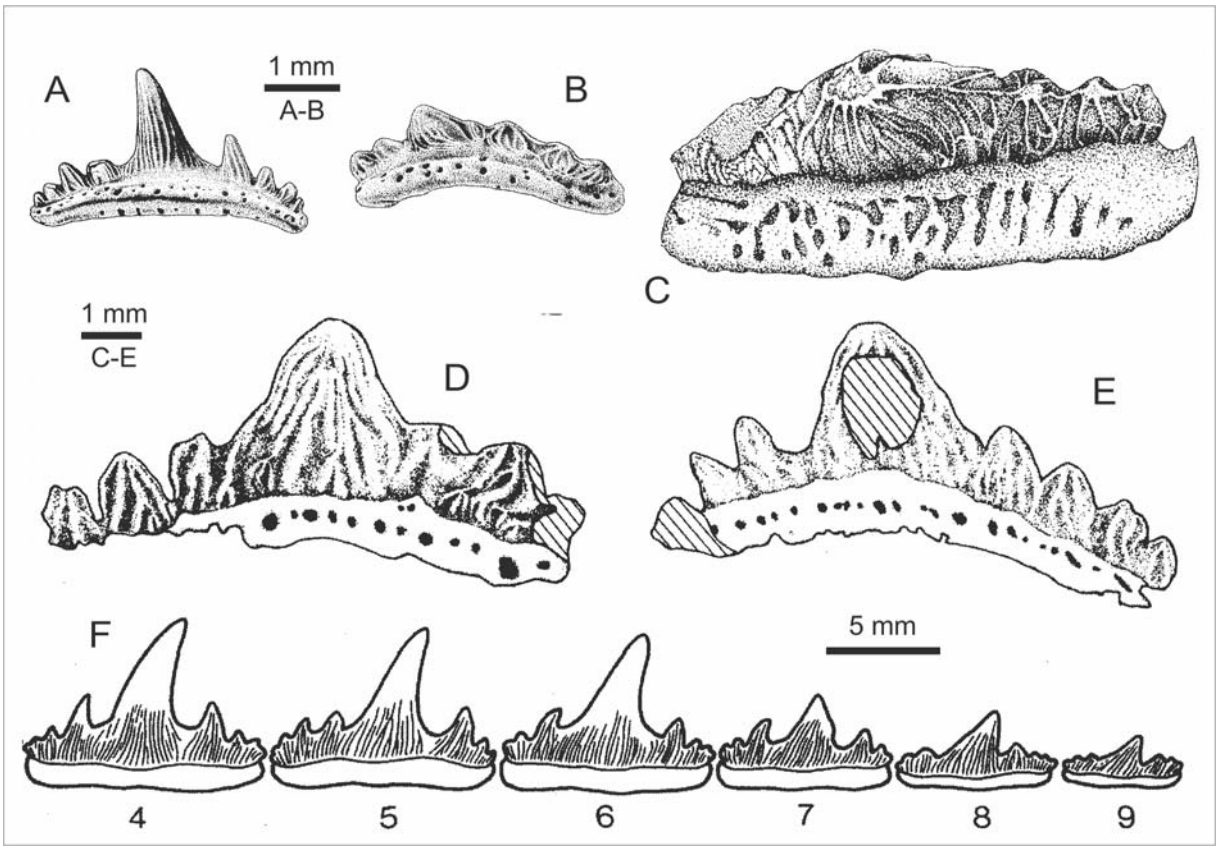
THE DENTITIONS OF CARBONIFEROUS EUSELACHII

Euselachians from Peru

The collection of Late Pennsylvanian shark teeth from Peru, Nebraska, housed at the Carnegie Museum, altogether a few hundred specimens, is much smaller than the collection described by Ossian (1974). Nevertheless, it appears to be a good representation of the diversity, at least as far as euselachian sharks are concerned. It is interesting that a few distinct forms, such as *Lissodus* sp. 1 and Euselachii indet. 2 went unnoticed by Ossian, although it is unbelievable that they were absent from his large collection. A whole range of euselachian dentition types is represented here: clutching dentition of *Ossianodus* gen. nov., but

Euselachian taxa	Number of specimens	Ossian's (1974) identification
Ossianodus nebraskensis sp. nov., high crown	22	*Hybodus nebraskensis* n.sp.
O. nebraskensis broad cusps	5	unreported
O. nebraskensis low crown	2	unreported
Lissodus sp. 1	11	unreported or, possibly, *Orodus hemiplicatus* n.sp. pl. 5, figs 3, 4
Lissodus sp. 2	1	unreported
Sphenacanthus tenuis sp. nov.	6	*Protacrodus* cf. *P. vetustus* pl. 4, figs 5, 6
Sphenacanthus carbonarius	3	*Protacrodus* cf. *P. vetustus* pl. 4, figs 1, 2
Euselachii gen. et sp. indet. 1	3	unreported
Euselachii gen. et sp. indet. 2	5	unreported
Total	58	

Table 1. The list of euselachian taxa from the Upper Pennsylvanian of Peru, Nebraska found in the collection of the Carnegie Museum, Pittsburgh, compared to the identifications made by Ossian (1974)



Text-fig. 8. *Ossianodus nebraskensis* gen. et sp. nov., CM 44547b, high-crown tooth. B. *O. nebraskensis*, CM 44547d, low-crown tooth. C. The largest tooth of *Sphenacanthus carbonarius* from the Upper Pennsylvanian of Pittsburgh, Pennsylvania (= holotype of *Hybodus allegheniensis* sensu Lund 1970; CM 19135a). D, E. Teeth of *Sphenacanthus serrulatus* from the Viséan of Scotland (NMS G 1976.70.1A and NMS G 1975.5.34B). F. Part of the dentition of *Egertonodus basanus* from the Lower Cretaceous of England; restoration based on the specimen AMNH 4692; 5-9, numbers of tooth-families, counting from the symphysis. Scale bars: A-E = 1 mm, F = 5 mm. C from Lund (1970), D-E from Dick (1998), F from Maisey (1983, part of fig. 18)

probably with some teeth able to crush; clutching-crushing type of *Sphenacanthus*; thoroughly crushing type of *Lissodus*; and probably crushing-grinding type of Euselachii indet. 2. Still, no cutting dentition is present. (See Duffin and Cuny 2008 for a possible explanation of the near absence of cutting teeth in non-selachimorph sharks.) The differences between the teeth in various positions are probably the greatest within the dentition of *Ossianodus* (see systematic section), but a certain degree of heterodonty is present in the other taxa as well.

According to Soler-Gijón (1997), based on his material from Puertollano Basin, Spain, the dentition of *Sphenacanthus carbonarius* is composed of two major types of teeth. The first, and the more common type, is represented by broad, protacrodont-like, relatively large, slightly asymmetrical teeth, with up to three or even four lateral cusps on each side. To the second, rare type belong narrow teeth with only one or two cusps on each side. Such narrow teeth are almost absolutely symmetrical and Soler-Gijón (1997, p. 155) suggested their anterior or even symphyseal position. The same diversity is observed in the material from the area of Pittsburgh, Pennsylvania, collected by Lund ("*Hybodus allegheniensis*" sensu Lund 1970; compare Text-figs 6F–H and 8C). However, among the teeth from Peru, only the first, broad type of *S. carbonarius* teeth is present. The absence of the narrow teeth in the material housed at the Carnegie Museum can be explained by their rarity, but it is less understandable why Ossian (1974) did not find them.

Another group of euselachian teeth, displaying certain differences but most probably belonging to the same species, is Euselachii indet. 2. Here, the heterodonty concerns the length of a tooth, number of lateral cusps and the prominence of the median cusp. Possibly the shorter teeth with the higher median cusp (e.g., Text-fig. 7H, I) were situated more anteriorly and the long, bar-like teeth (Text-fig. 7E) more posteriorly in the jaw.

The teeth of *Sphenacanthus tenuis* sp. nov., at least those found thus far, do not differ much in size, but some of them are absolutely symmetrical, with the cusps directed upwards (Text-fig. 5A), and the other have all the cusps somewhat inclined distally (posteriorly, Text-fig. 5E). Again, the former are probably from the anterior part, and the latter from the lateral part of the jaw.

The least heterodont species of the described here is *Lissodus* sp. 1. The shape of the crown is very similar in all the specimens and the observed differences in height of the median cusp are probably the result of abrasion. All the teeth are virtually symmetrical.

General remarks

There are very few Carboniferous euselachian sharks whose articulated, at least partial, dentitions are known. Actually, this concerns only two species: *Hamiltonichthys mapesi* Maisey, 1989, from the Gzhelian of Kansas and *Onychoselache traquairi* Dick, 1978, from the Viséan of Scotland. However, some help in the attempts to restore the dentitions of other taxa can be obtained from Mesozoic analogues, such as *Hybodus*, *Egertonodus, Acrodus* or *Lissodus*. It appears that most of Carboniferous euselachian dentitions served to crush or even grind hard prey, even if a few anterior teeth had some potential to grasp it. The only taxa that break this rule are *Ossianodus nebraskensis* gen. et sp. nov. (predominantly high-crowned, clutching teeth) and *Cooleyella fordi* (Duffin and Ward, 1983), possibly a neoselachian, whose sharp teeth probably could also cut.

As far as heterodonty is concerned, a few types can be proposed (in brackets, better known and named Carboniferous euselachian taxa representing particular types):

1. *Hybodus*-type – anterior and lateral teeth with high, hybodont-type crowns; anterior teeth symmetrical, lateral teeth with the cusps inclined distally; posterolateral teeth with low, protacrodont-type crowns, strongly asymmetrical (*Ossianodus* gen. nov.).

2. *Sphenacanthus*-type – all teeth with protacrodont-type crowns, with a degree of asymmetry and distal inclination of cusps increasing postero-laterally; a few teeth near the symphysis may be significantly narrower (*Sphenacanthus,* possibly *Tristychius* Agassiz, 1837).

3. *Lissodus*-type – all teeth virtually symmetrical, with the cusps largely fused; the differences between the teeth concern their width and the height of the median part; the highest and narrowest teeth situated anteriorly (*Lissodus, Onychoselache*, ?*Acrodus olsoni* and ?*A. sweetlacruzensis* sensu Johnson 1981).

4. *Hamiltonichthys*-type – anterior teeth narrow and symmetrical; lateral teeth broad, with the highest part not in the median position, but displaced mesially; a few posterolateral teeth (in *Hamiltonichthys*) narrower; the cusps usually low and fused (*Hamiltonichthys*, *Cassisodus* Ginter and Sun, 2007).

The dentitions of the earliest, Devonian euselachians, represent only the second and third types. Late Famennian *Protacrodus serra* (Ginter *et al*. 2010, fig. 80A–C), probably has narrow, blade-like anterior teeth and asymmetrical, broad laterals, characteristic of the *Sphenacanthus*-type. Other well known Late Devonian taxa, *Lissodus lusavorichi* (Ginter *et al.* 2011), *Roongodus* (Hairapetian and Ginter 2009), and *Deihim* (Ginter *et al*. 2010, fig. 81) are more or less typical of the *Lissodus*-type. However, the teeth of Frasnian-Famennian *Protacrodus vetustus* (see Gross 1938; Ginter *et al*. 2010, fig. 79), a model species for the protacrodont crown, do not fit well in the above subdivision. They appear to be symmetrical throughout the dentition; the only difference between the teeth in different positions lies in their size and the number of lateral cusps. This would make *P. vetustus* a representative of the *Lissodus*-type, but its cusps are much less fused than in *Lissodus*.

On the other hand, most of the described Permian non-neoselachian euselachian Chondrichthyes have dentitions comparable to the third or fourth type. The *Lissodus*-type is represented by quite a few of them, such as *Reesodus* and *Khuffia* from Oman (Koot *et al*. 2013) or *Lissodus sardiniensis* (Fischer *et al*. 2010). The only one with the *Hamiltonichthys*-type of heterodonty which I encountered in the literature is *Omanoselache* (Koot *et al*. 2013).

CONCLUSIONS

Despite the disarticulated state of the material from Peru, Nebraska, it gives an interesting insight into the diversity of dentition forms in Late Carboniferous euselachian sharks. A few patterns continue from the Early Carboniferous or even Devonian, but there are also certain innovations, characteristic rather of the Mesozoic, such as the hybodont-like dentition of *Ossianodus* gen. nov. One might argue that the clutching teeth of *Ossianodus* and later hybodonts are nothing more than a return, in a modified style, to the functionally cladodont dentition. However, the probable presence of crushing, protacrodont-like teeth in the posterolateral position is defi-

nitely new. The complete absence of neoselachian cutting teeth in the material indicates that even if the latter group already has existed, its occurrence was very restricted.

Acknowledgments

I am grateful to Dr. Richard Lund (Carnegie Museum of Natural History) for driving me across Pennsylvania to Pittsburgh and for his assistance at the Carnegie Museum. My research in USA in 2003 was financed by the Polish-American Fulbright Comission scholarship and the preparation of the paper by the Institute of Geology grant (BSt 170202). Warm thanks are due to the reviewers, Gilles Cuny (Université Claude Bernard, Lyon) and Christopher J. Duffin (Sutton, Surrey), for their insightful comments and corrections which greatly improved the manuscript.

REFERENCES

Agassiz, L.J.R. 1833–1843. Recherches sur les poissons fossiles, vol. 3, pp. 8 + 390 + 32. Petitpierre; Neuchâtel et Soleure.

Archer, A.W., Lanier, W.P. and Feldman H.R. 1994. Stratigraphy and depositional history within incised-paleovalley fills and related facies, Douglas Group (Missourian/Virgilian; Upper Carboniferous) of Kansas, USA. In: R.W. Dalrymple, R. Boyd and B.A. Zaitlin (Eds), Incised-valley systems: Origin and Sedimentary Sequences. SEPM Special Publication, **51**, 353–368.

Bonaparte, C. 1832-41. Iconografia della Fauna Italica per le quatro Classi degli Animali Vertebrati. Tomo 3: Pesci, pp. 1–266. Salviucci; Rome.

Brough, J. 1935. On the Structure and relationships of the Hybodont sharks. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society*, **79**, 35–49.

Brown, C. 1900. Ueber das Genus *Hybodus* und seine systematische Stellung. *Palaeontographica*, **46**, 149-174.

Cappetta, H. 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In: H.-P. Schultze (Ed.), Handbook of Paleoichthyology, 3E, pp. 1–512. Friedrich Pfeil; München.

Davis, J.W. 1883. On the fossil fishes of the Carboniferous Limestone Series of Great Britain. *Transactions of the Royal Dublin Society*, 2nd series, **1**, 327–548.

Dick, J.R.F. 1978. On the Carboniferous shark *Tristychius arcuatus* Agassiz from Scotland. *Transactions of the Royal Society of Edinburgh*, **70**, 63–109.

Dick, J.R.F. 1998. *Sphenacanthus*, a Palaeozoic freshwater shark. In: D.B. Norman, A.R. Milner and A.C. Milner (Eds), A study of fossil vertebrates. *Zoological Journal of the Linnean Society*, **122**, 9–25.

Duffin C.J. and Cuny G. 2008. *Carcharopsis prototypus* and the adaptations of single crystallite enameloid in cutting dentitions. *Acta Geologica Polonica*, **58**, 181–184.

Duffin, C.J. and Ward, D.J. 1983. Neoselachian sharks teeth from the Lower Carboniferous of Britain and the Lower Permian of the U.S.A. *Palaeontology,* **26**, 93–110.

Egerton, P.M.G. 1845. Description of the mouth of a *Hybodus* found by Mr. Boscawen Ibbetson in the Isle of Wight. *Quarterly Journal of the Geological Society of London*, **1**, 197–199.

Fischbein, S.A., Fielding, C.R. and Joeckel, R.M. 2009. Fluvial-estuarine reinterpretation of large, isolated sandstone bodies in epicontinental cyclothems, Upper Pennsylvanian, northern Midcontinent, USA, and their significance for understanding late Paleozoic sea-level fluctuations. *Sedimentary Geology* **216**, 15–28.

Fischer, J., Schneider, J.W. and Ronchi, A. 2010. New hybondontoid shark from the Permocarboniferous (Gzhelian–Asselian) of Guardia Pisano (Sardinia, Italy). *Acta Palaeontologica Polonica* **55**, 241–264.

Giebel, C.G. 1848. Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere. Bd. 1: Wirbelthiere. Abt. **3**: Fische, pp. 1–467. Brockhaus; Leipzig.

Ginter, M., Hairapetian, V. and Grigoryan, A. 2011. Chondrichthyan microfossils from the Famennian and Tournaisian of Armenia. *Acta Geologica Polonica*, **61**, 153–173. Warszawa.

Ginter, M., Hampe, O. and Duffin, C.J. 2010. Chondrichthyes. Paleozoic Elasmobranchii: Teeth. In: H.-P. Schultze (Ed.), Handbook of Paleoichthyology 3D, pp. 1–168. Friedrich Pfeil; München.

Ginter, M. and Sun, Y. 2007. Chondrichthyan remains from the Lower Carboniferous of Muhua, southern China. *Acta Palaeontologica Polonica*, **52**, 705–727.

Gross, W. 1938. Das Kopfskelett von *Cladodus wildungensis* Jaekel. 2. Teil: Der Kieferbogen. Anhang: *Protacrodus vetustus* Jaekel. *Senckenbergiana*, **20**, 123–145.

Hairapetian, V. and Ginter, M. 2009. Famennian chondrichthyan remains from the Chahriseh section, central Iran. *Acta Geologica Polonica*, **59**, 173–200.

Hay, O.P. 1902. Bibliography and catalogue of the fossil vertebrata of North America. *US Geological Survey Bulletin*, **179**, 1–868.

Herman, J. 1977. Les sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes: Eléments d'une biostratigraphie intercontinentale. *Mémoires pour servir à l'explication des Cartes géologiques et minières de la Belgique*, **15**, 1–450.

Huxley, T.H. 1880. A manual of the anatomy of vertebrated animals, pp. 1–431. D. Appleton; New York.

Johnson, G.D. 1981. Hybodontoidei (Chondrichthyes) from the Wichita-Albany Group (Early Permian) of Texas. *Journal of Vertebrate Paleontology*, **1**, 1–41.

Koot, M.B., Cuny, G., Tintori, A. and Twitchett, R.J. 2013. A new diverse fauna from the Wordian (Middle Permian) Khuff Formation in the interior Haushi-Huqf area, Sultanate of Oman. *Palaeontology,* **56**, 303–343.

Lund, R. 1970. Fossil fishes from southwestern Pennsylvania. Part 1: Fishes from the Duquesne Limestones (Conemaugh, Pennsylvanian). *Annals of Carnegie Museum*, **41**, 231-261.

Maisey, J.G. 1975. The interrelationships of phalacanthous selachians. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **9**, 563–567.

Maisey, J.G. 1982. Studies on the Paleozoic selachian genus *Ctenacanthus* Agassiz: No. 2. *Bythiacanthus* St. John and Worthen, *Amelacanthus*, new genus, *Eunemacanthus* St. John and Worthen, *Sphenacanthus* Agassiz, and *Wodnika* Münster. *American Museum Novitates*, **2722**, 1–24.

Maisey, J.G. 1983. Cranial anatomy of *Hybodus basanus* Egerton from the Lower Cretaceous of England. *American Museum Novitates*, **2758**, 1–64.

Maisey, J.G. 1987. Cranial anatomy of the Lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with comments on hybodontid systematics. *American Museum Novitates*, **2878**, 1–39.

Maisey, J.G. 1989. *Hamiltonichthys mapesi*, g. & sp. nov. (Chondrichthyes; Elasmobranchii), from the Upper Pennsylvanian of Kansas. *American Museum Novitates*, **2931**, 1–42.

Ossian, C.R. 1974. Paleontology, paleobotany and facies characteristics of a Pennsylvanian delta in Southeastern Nebraska. Unpublished Ph.D. dissertation, University of Texas, Austin, pp. 1-20 + 1-393, available at: https://www.academia.edu/1424478

Owen, R. 1846. Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals. Part 1. Fishes, pp. 11 + 304. Longman, Brown, Green, and Longmans; London.

Rees, J. 2008. Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology – preliminary results. *Acta Geologica Polonica*, **58**, 217-221.

Rees, J. and Underwood, C. 2002. The status of the shark genus *Lissodus* Brough, 1935, and the position of the nominal *Lissodus* species within the Hybodontoidea (Selachii). *Journal of Vertebrate Paleontology*, **22**, 471–479.

Soler-Gijón, R. 1997. Euselachian sharks from the Late Carboniferous of the Puertollano Basin, Spain: biostratigraphic and palaeoenvironmental implications. *Modern Geology*, **21**, 137–169.

St. John, O. and Worthen, A. H. 1875. Description of fossil fishes. *Geological Survey of Illinois, Paleontology,* **6,** 245–488.

Manuscript submitted: 20th January 2016
Revised version accepted: 15th July 2016